

Evolution of the entrance rate and of the spatio-temporal distribution of Lessepsian Mollusca in the Mediterranean Sea

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The evolution of the entrance rate of Lessepsian Mollusca into the Mediterranean Sea as well as the development of their spatio-temporal dispersal were investigated, based on literature data and intensive sampling, off the coasts of Cyprus, SW Turkey and the Aegean coasts of Greece and Turkey. Based on our results, 130 species of Mollusca (1 species of Polyplacophora, 84 species of Gastropoda, 41 species of Bivalvia and 4 species of Cephalopoda) can be considered as verified Lessepsian migrants. Analysis of data revealed that there is an acceleration of the entrance rate of Lessepsian molluscs (similar pattern with Lessepsian Decapoda), which is statistically significant. Furthermore, there is a progressive dispersal of Lessepsian molluscs from Port Said to the west, along the African coast, and to the east along the coasts of Israel, Lebanon, and Syria, from there towards the southern Turkish coasts and the coasts of Cyprus, and finally towards the Greek and Turkish Aegean coasts. The increasing trend in the entrance rate of thermophilous Lessepsian Mollusca as well as their progressive dispersal towards higher latitudes could be attributed to the observed, gradual increase in temperature of the Mediterranean waters.

Key words: Lessepsian migration, Mollusca, Mediterranean Sea.

INTRODUCTION

The first review of the phenomenon of Lessepsian migration was given by Por (1978). In his review, he reported 44 species of Lessepsian Mollusca (27 of high and 17 of low probability) and provided information on their distribution in the Mediterranean Sea. According to Por (1978), Lessepsian molluscs are shallow-water species of Indo-Pacific origin which have actively entered the Mediterranean after successfully colonizing the Suez Canal.

Later, Por & Dimentman (2006) provided an updated review of the Lessepsian migration refuting certain of the views set forth by Por (1978). These authors noted that Lessepsian migration is a duplication of a natural and active process of species area ex-

pansion. Hence, species of Indo-Pacific origin which are newly recorded in the Mediterranean Basin but have most probably been transported passively by human navigational means or by aquaculture should not be treated as “true” Lessepsian migrants, but rather as introduced non-indigenous species.

Since the review of Por (1978) a significant amount of information has been published on Lessepsian Mollusca (e.g. Barash & Danin, 1982, 1986; van Aartsen *et al.*, 1989, 1990; Koutsoubas, 1992; Buzzurro & Greppi, 1995, 1996; Koutsoubas & Cinelli, 1996; Zenetos *et al.*, 2003, 2005, 2009a,b,c, 2011; Mienis, 2004a, 2008; Galil, 2006, 2009; Koutsoubas *et al.*, 2007; Katsanevakis *et al.*, 2009). Galil (2006), reviewing the erythrean invasion, listed 139 species of Lessepsian Mollusca in the Mediterranean Sea. Three years later, Galil (2009) listed 175 molluscs of Indo-Pacific origin in the Mediterranean. However, 46 of these should not be considered Lessepsian migrants,

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since they were introduced in the Mediterranean by maritime transportation.

The review of the relevant literature shows that although there is a significant amount of data on the geographical distribution of Lessepsian molluscs, there is no information on their entrance rate in the Mediterranean or the evolution of their spatio-temporal dispersal. Por (1978) treating all Lessepsian groups as one heterogeneous unit, noted that there were no indications at that time that the Lessepsian migration had been speeding up and the processes seemed to tend to an asymptotic equilibrium. Recently, Por & Dimentman (2006) noted that the previous assumption of Por (1978) had not been proved correct after a quarter of a century.

On the other hand, there is now evidence that during the last 80 years, the entrance rate of different Lessepsian groups in the Mediterranean is accelerating. Tzomos *et al.* (2007) and Ben Rais Lasram & Mouillot (2009) have clearly demonstrated that there is an increase in the entrance rate of Lessepsian fish in the Mediterranean while there is also a gradual dispersal of these species towards higher geographical latitudes. Also, Koukouras *et al.* (2010) have reached similar results in respect to Lessepsian Decapoda. The accelerating entrance rates of these Lessepsian groups as well as their significant dispersal have been linked with the gradual increase in the temperature of the Mediterranean waters, a phenomenon reflecting the ongoing climate change (Béthoux *et al.*, 1990; Boero *et al.*, 2008; Ben Rais Lasram & Mouillot, 2009).

The aims of this study were: (i) to quantify the entrance rate of Lessepsian Mollusca into the Mediterranean Sea, (ii) to reveal a possible pattern in the spatio-temporal dispersal of these species in the Mediterranean Sea, and (iii) to identify potential factors that determine the intensity of the entrance rate and the dispersal of the species of Lessepsian molluscs.

MATERIALS AND METHODS

In order to gather more data on the Lessepsian molluscs, a suitable network of sampling stations was designed focusing on areas of inadequate sampling. The locations of the 25 sampling stations selected are given in Figure 1. Sampling was carried out during 2004 and 2005, with all available sampling gear (trawl nets, hanging nets, fishing traps, free diving and SCUBA diving) depending on the type of habitat.

In order to perform the spatial analysis of the data collected, the following five geographical areas, sit-

uated on the Lessepsian migration routes were determined: 1, PS (Port Said up to the Syrian-Turkish border); 2, ST (southern Turkish coast, west of the Syrian-Turkish border to the Gulf of Fethiye); 3, CY (Cyprus); 4, AS (Greek and Turkish Aegean Sea coasts, north of Fethiye Gulf) and 5, NA (North African coast). Moreover, we investigated the spatio-temporal dispersal of Lessepsian Mollusca towards the Central Mediterranean (CM, delimited to west by the Strait of Sicily and to the east by Crete Island, excluding the northern African coast), the Adriatic Sea (AD, north of the Strait of Otranto) and the West Mediterranean (WM, west of the Strait of Sicily).

Based on the literature collected and the sampling data obtained, Table 1 was constructed in which all verified species of Lessepsian Mollusca were included. In all estimates made, where possible, the year of collection of a species was considered instead of the year of publication of the relevant information.

For each one of the five designated areas of the eastern Mediterranean, the total number of species of Lessepsian Mollusca reported so far was estimated. Furthermore, the number of species in each area was estimated for two periods: from 1869 to 1990 and from 1990 onwards. The year 1990 was chosen as a cut-off point, since there were few records (only 8 species) of Lessepsian molluscs from the Aegean Sea before that year. Furthermore, the relevant sampling effort seems to be more intensive in all areas from that year onwards (see references in Table 1).

For estimating the annual, numerical accumulation of the Lessepsian molluscs, the period from 1954 to 2009 was chosen. It should be noted that prior to 1954, there were very few studies on the Lessepsian molluscs in the Mediterranean and thus the relevant data were not considered reliable to make estimates on the numerical accumulation of species. For the time period 1954-2009, the cumulative numbers of Lessepsian Mollusca were estimated per year and then plotted against time. The data thus compiled were assessed using regression analysis.

The entrance rate of Lessepsian Mollusca (number of new species per 15 years) was estimated for the period 1869 (opening of the Suez Canal) up to 2003. This period was divided into 9 consecutive 15-year intervals. For each of these, the number of new mollusc species that entered the Mediterranean via the Lessepsian route was calculated. The division into 15-year intervals was intended to decrease the high variation in the number of new Lessepsian molluscs per

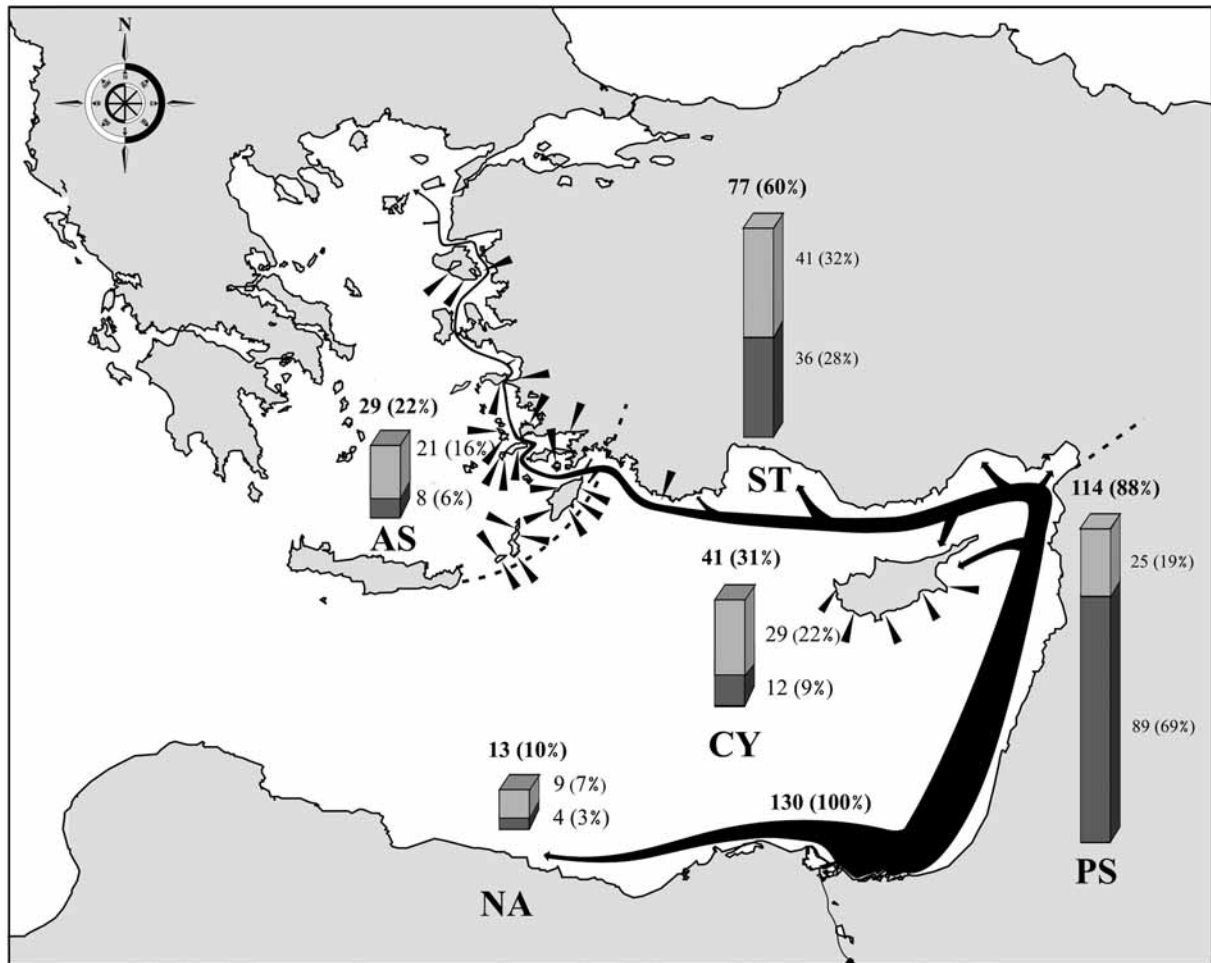


FIG. 1. The sampling locations during the present study indicated by black triangles. Geographical distribution of the Lessepsian Mollusca (in absolute numbers and in percentages of their total number) in the five areas here recognized, and for two time periods: 1869-1990 (lower, dark part of the column) and 1990-onwards (upper, light part of the column). The black, thinning zone and arrows show the probable route of the expansion of the Lessepsian molluscs. The thickness of the zone indicates the number of species. Abbreviations: PS: Port Said up to the Syrian-Turkish border; ST: southern Turkish coast; CY: Cyprus; AS: Greek and Turkish Aegean Sea coasts; NA: north African coast.

year, an obvious result of the different intensity in sampling efforts. The assessment of entrance rate over time was performed using regression analysis.

RESULTS

In total, 130 species of Mollusca (1 species of Polyplacophora, 84 species of Gastropoda, 41 species of Bivalvia and 4 species of Cephalopoda) can be considered as verified Lessepsian migrants. These species are given in Table 1, along with their distribution in the geographical areas of the Mediterranean as defined herein.

Figure 2 shows the annual numerical accumulation of Lessepsian Mollusca for the period 1954 to 2009. The linear regression trend (given by: $y =$

$1.9809x - 3846.3$) shows a statistically significant ($p < 0.001$) increase of their cumulative number per year. That is, every year, on average, approximately 2 Lessepsian mollusc species are entering the Mediterranean Sea.

Changes in the entrance rate of the Lessepsian Mollusca (number of new species per 15 years) for the period 1869 to 2003 are shown in Figure 3. The linear regression trend (given by: $y = 0.2922x - 553.68$) shows a statistically significant ($p < 0.001$) increase of the entrance rate in relation to time. That is, in every consecutive fifteen-year interval the number of new Lessepsian mollusc species entering the Mediterranean is on average higher than the previous fifteen-year interval.

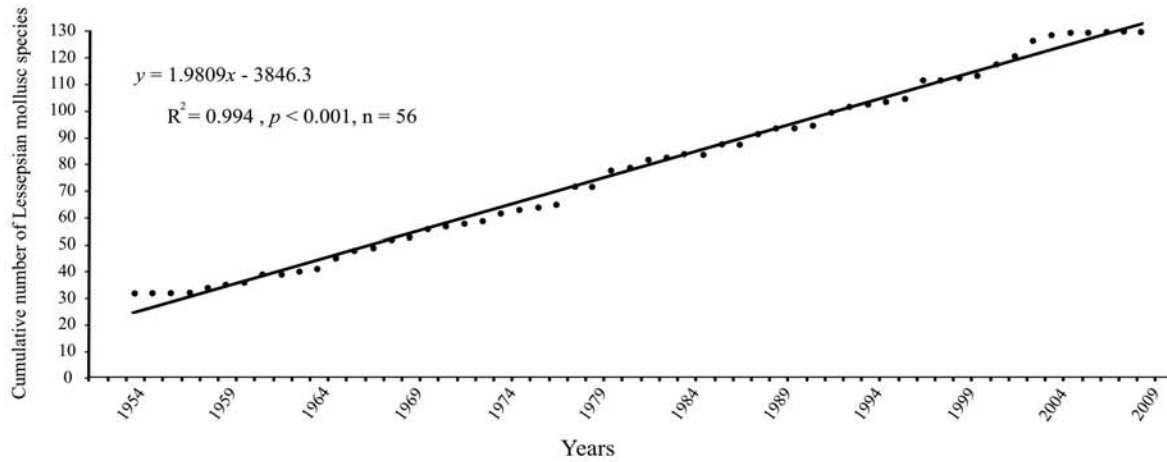


FIG. 2. Annual numerical accumulation of Lessepsian Mollusca from 1954 up to 2009.

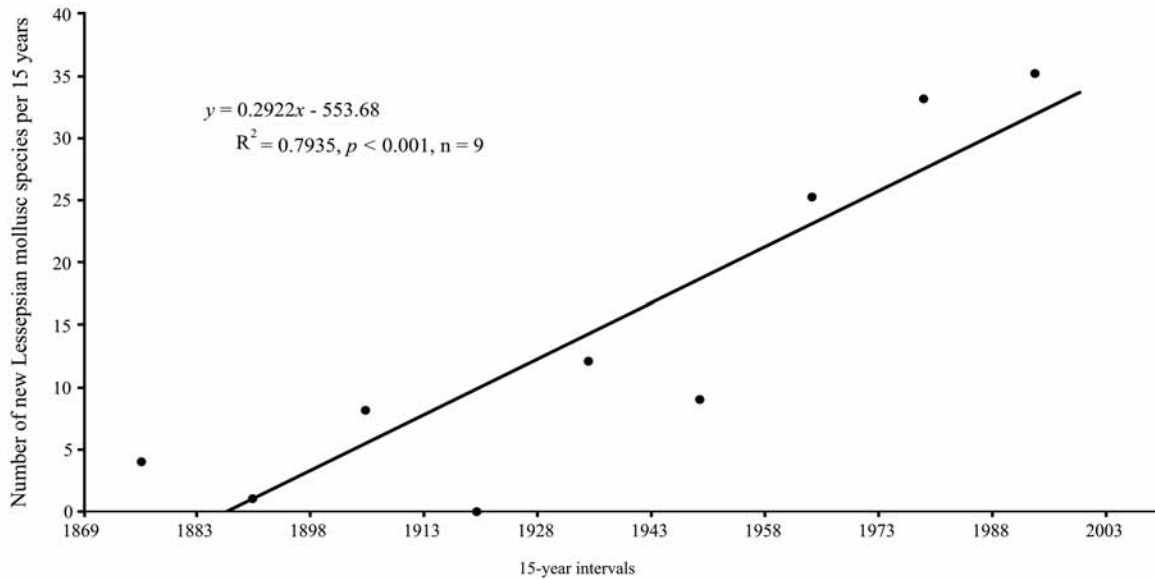


FIG. 3. Change of the entrance rate (number of new species per fifteen years) in the nine consecutive fifteen-year intervals for the period 1869-2003.

The annual numerical accumulation of the number of Lessepsian Mollusca in five geographical areas of the eastern Mediterranean and in the Mediterranean as a whole is shown in Figure 4. Area PS, the area closest to Port Said, hosts the highest number of species (114), and their presence has been reported starting 1874, that is 5 years after the opening of the Suez Canal. Area NA, to the west of Port Said and directly neighboring as well, hosts a much lower number of species (13) reported from 1869 onwards. The area ST beyond PS, hosts less species (77) than the latter. Moreover, the presence of these species was not reported before 1958. Cyprus (CY), geographi-

cally isolated and separated from the neighboring mainland, hosts a lower number of Lessepsian Mollusca than area ST (41 species) and their presence has been reported starting in 1899. Finally, the Greek and Turkish Aegean Sea coasts (AS) host the lowest number of Lessepsian species (29) with the exception of NA, while recording Lessepsian molluscs has started there in 1939.

Based on the above, it is apparent that the time required for the dispersal of Lessepsian molluscs from Port Said towards the five geographical areas is related to the shoreline distance of the areas from Port Said. Thus, in areas located further away, the ac-

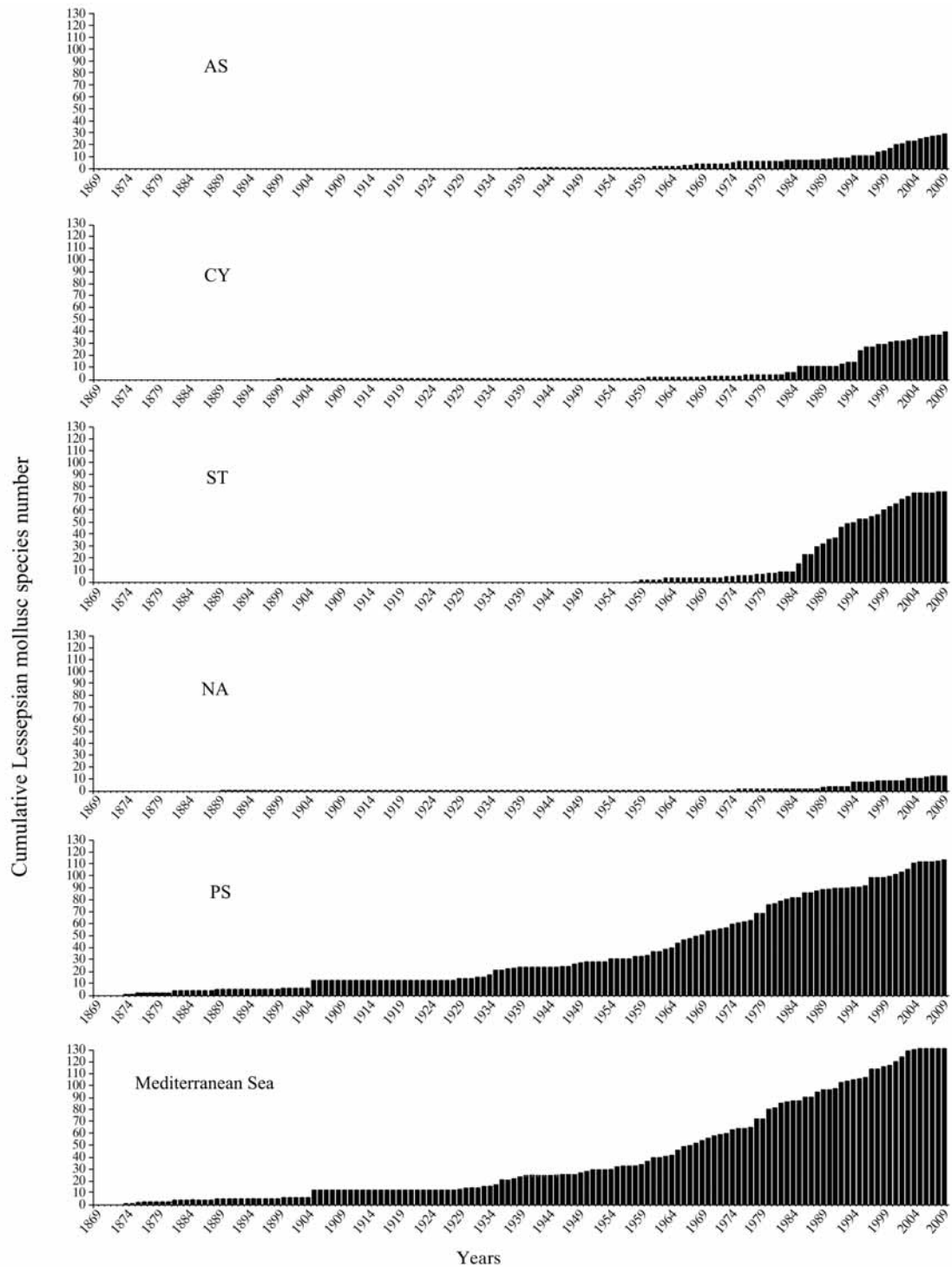


FIG. 4. Annual numerical accumulation of Lessepsian Mollusca in the five geographical areas here recognized, and also in the Mediterranean Sea as a whole. Abbreviations as in Figure 1.

cess of Lessepsian molluscs is happening with an analogous time delay. Minor deviations from this pattern should be attributed to the different intensity of the sampling effort carried out in each area.

Figure 1 demonstrates the distribution of the Lessepsian Mollusca in the five designated geographical areas of the eastern Mediterranean. As demonstrated, the total number of known species is decreasing from

TABLE 1. Lessepsian mollusc species in the Mediterranean and their distribution in the five designated eastern Mediterranean areas, the Adriatic Sea, the central, and the western Mediterranean. For each species, the first collection year for each area is given as well as relevant literature references. Abbreviations: PS: Port Said up to the Syrian-Turkish border; ST: southern Turkish coast; CY: Cyprus; AS: Greek and Turkish Aegean Sea coasts; NA: north African coast; AD: Adriatic Sea; CM: central Mediterranean (excluding the northern African coast); WM: western Mediterranean; *: species collected during the present study

	PS	ST	CY	AS	NA	AD	CM	WM	References
POLYPLACOPHORA									
<i>Chiton hululensis</i> (E.A. Smith in Gardiner, 1903)	1934								Barash (1973)
GASTROPODA									
<i>Aeteocina crithodes</i> Melvill & Standen, 1907		2003							Mienis (2004a)
<i>Aeteocina mucronata</i> (Philippi, 1849)	1986	1986	1992	1991	1989				Zenetos et al. (2003)
<i>Amathina tricarinata</i> (Linnaeus, 1767)	2000	2000							Çeviker & Albayrak (2006)
<i>Angiola punctostriata</i> (E.A. Smith, 1872)	1950								Mienis (1980a)
<i>Amys cylindricus</i> (Hebling, 1779)	2002								Mienis (2004a)
<i>Bulla arabica</i> Malaquias & Reid, 2008	1978	1992	2000	1998	2007				Zenetos et al. (2003, 2011)
<i>Caloria indica</i> (Bergh, 1896)	1986								Gat (1993)
<i>Cellana rota</i> (Gmelin, 1791)	1961			1989					Zenetos et al. (2003, 2009c)
<i>Cerithidium diplax</i> (Watson, 1886)	1961	1986							van Aartsen (2006)
<i>Cerithidium perparvulum</i> (Watson, 1886)	2004	1986	1995						van Aartsen (2006)
<i>Cerithopsis pubis</i> (Issel, 1869)	1978	1989	1985						Zenetos et al. (2003)
<i>Cerithopsis tenthrenois</i> (Melvill, 1896)	1982	<1990	1985						Zenetos et al. (2003)
<i>Cerithium columnna</i> Soweby, 1834	1996								Mienis (2003a)
<i>Cerithium egenum</i> Gould, 1849	1971								Mienis (2001a)
<i>Cerithium nesioticum</i> Pilsbry & Vanatta, 1906	1970		1985						Zenetos et al. (2003)
* <i>Cerithium scabridum</i> Philippi, 1848	1882	1985	1983	1998	1997		<1978	1976	Tzomos (2007), Zenetos et al. (2009b), Antit et al. (2011)
<i>Chelidonura fulvipunctata</i> Baba, 1938	1986	1959					1993		Zenetos et al. (2003)
<i>Chromodoris annulata</i> Eliot, 1904	2009	2008	2009	2003					Gökoğlu & Özgür (2008), Zenetos et al. (2011)
<i>Chromodoris quadricolor</i> (Rüppell & Leuckart, 1830)		2004			2003			1982	Zenetos et al. (2006)
<i>Chrysallida fischeri</i> (Hornung & Mermod, 1925)	1974	1988				1993			Öztürk & Can (2006)
<i>Chrysallida maiiae</i> (Hornung & Mermod, 1924)	1935	1963	1995						Zenetos et al. (2003)
<i>Chrysallida micronana</i> Öztürk & van Aartsen, 2006		1997		2000					Zenetos et al. (2003)
<i>Chrysallida pirinthella</i> (Melvill, 1910)	1982	1988							Öztürk & van Aartsen (2006)
<i>Cingulina isseli</i> (Tryon, 1886)	1980	1986	1998						Zenetos et al. (2003)
<i>Clypeomorvus bifasciatus</i> (Sowerby G.B II, 1855)	1983				1994				Zenetos et al. (2003)
<i>Cycloscala hyalina</i> (Sowerby G.B. II, 1844)		1995	1992						Zenetos et al. (2003)

TABLE 1. continued

	PS	ST	CY	AS	NA	AD	CM	WM	References
<i>Cyllichina girardi</i> (Audouin, 1826)	1974	1990	1996	1994					Zenetos et al. (2003)
<i>Dendrodoris fumata</i> (Rüppell & Leuckart, 1830)	1980								Barash & Danin (1986)
<i>Diala varia</i> A. Adams, 1861	1935	2002							Zenetos et al. (2003)
<i>Diodora ruppellii</i> (Sowerby G.B. I, 1835)	<1948	1985							Galil (2009)
<i>Engina mendicaria</i> (Linnaeus, 1758)	2001								Mienis (2004a)
<i>Ergatata contracta</i> (Reeve, 1846)	2001								Mienis (2004a)
<i>Ergatata junionae</i> Houart 2008	2004	1992	1993	2002					Zenetos et al. (2008)
<i>Erosaria turdus</i> (Lamarek, 1810)	1980				2003		2005		Galil (2009)
<i>Finella pupoides</i> A. Adams, 1860	1958	1958	<1996	2001					Öztürk & Can (2006)
<i>Flabellina rubrolineata</i> (O'Donoghue, 1929)	1988	2001	2003						Zenetos et al. (2003)
<i>Fusinus verrucosus</i> (Gmelin, 1791)	1882								Zenetos et al. (2003)
<i>Gibborissoa virgata</i> (Philippi, 1849)	1970	1997							van Aartsen (2002)
<i>Haliotis pustulata cruenta</i> Reeve, 1846	1961				1994				Zenetos et al. (2003)
<i>Haminoea cyanomarginata</i> Heller & Thompson, 1983		2002		2001			2006		Crocetta & Vazzana (2008)
<i>Hinemoa cylindrica</i> (de Folin, 1879)		1992							Buzzurro et al. (2001)
<i>Hypselodoris infucata</i> (Rüppell & Leuckart, 1830)	1965	1999							Özvarol et al. (2010)
<i>Leucotina eva</i> Thiele, 1925		1995		2000					Ginar et al. (2011)
<i>Leucotina natalensis</i> Smith E.A. 1910	1978	1986	<1996						Galil (2009)
<i>Lienardia mighelsi</i> Iredale & Tomlin, 1917				<2003					Cinar et al. (2005)
<i>Metaxia bacillum</i> (Isse, 1869)	1978	1992	<1995						Zenetos et al. (2003)
<i>Monotigma lauta</i> (A. Adams, 1853)	1967	1988							Galil (2009)
<i>Murchisonella columna</i> (Hedley, 1907)	1997	1993							Zenetos et al. (2003)
<i>Murex forskoehtii</i> Röding, 1798	<1905			1966					Settepassi (1967)
<i>Nassarius arcularia pilcatus</i> (Röding, 1798)	1968								Barash & Danin (1977)
<i>Nerita sanguinolenta</i> Menke, 1829		2004		1968	1994				Zenetos et al. (2003), Mutaf et al. (2007)
<i>Notocochlis gualteriana</i> (Récluz, 1844)	1966						1996		Galil (2009)
<i>Odostomia lorioli</i> (Hornung & Mermod, 1924)	1974								van Aartsen (1987)
<i>Oscilla jocosa</i> Melvill, 1904	1984								van Aartsen et al. (1989)
<i>Oxynoe viridis</i> (Pease, 1861)		2002							Galil (2009)
<i>Palmadusta lentiginosa</i> (Gray, 1825)	1989								Mienis (1990)
<i>Planaxis savignyi</i> Deshayes 1844	<1905								Galil (2009)
<i>Pleurobranchus forskalii</i> Rüppell & Leuckart, 1828	1975								Barash & Danin (1977)
<i>Plocamopherus ocellatus</i> Rüppell & Leuckart, 1828	1977	1998							Yokes & Rudman (2004)

TABLE 1. continued

	PS	ST	CY	AS	NA	AD	CM	WM	References
<i>Pseudominolia nedyma</i> (Melvill, 1897)	1966	1992							Zenetos et al. (2003)
<i>Purpuradusta gracilis notata</i> (Gill, 1858)	1981	1982	2000						Zenetos et al. (2009a)
<i>Pyrrunculus fourieri</i> (Audouin, 1826)	1986	<1989	1995						Galil (2009)
<i>Retusa desgenettii</i> (Audouin, 1826)	1969								Mienis (2004b)
<i>Rhinoclavis kochi</i> (Philippi, 1848)	1963	1985	1976		1975				Galil (2009)
<i>Rhinoclavis sinensis</i> (Gmelin, 1791)	2003								Mienis (2004a)
<i>Rissoina ambigua</i> (Gould, 1849)	1958	1985	1985						Mienis (2004a)
<i>Rissoina bertholleti</i> Issel, 1869	<1997								Zenetos et al. (2003)
<i>Rissoina spirata</i> Sowerby G.B. I, 1820	1954							1990	Giannuzzi-Savelli et al. (1997)
<i>Sabia conica</i> (Schumacher, 1817)	1965	1999							Barash & Danin (1986)
<i>Siphonaria crenata</i> de Blainville, 1827	1965	1999							Zenetos et al. (2003)
<i>Smaragdia souverbiana</i> (Montrouzier, 1863)	2004	1992	1995						Zenetos et al. (2003)
<i>Sticteulima lentiginosa</i> (A. Adams, 1861)	2004	1989	1995						Zenetos et al. (2003)
<i>Stomatella impertusa</i> (Burrow, 1815)	1991	1999							Galil (2009)
<i>Strombus mutabilis</i> Swainson, 1821	1983	1978	1985	1983	2006	1996			Zenetos et al. (2003)
* <i>Strombus persicus</i> Swainson, 1821									Mienis (2001b)
<i>Syrnola cinctella</i> A. Adams, 1860	1949	1963	1995	2001					Ben Souissi & Zaouali (2007), Tzomos (2007)
<i>Syrnola fasciata</i> Jickeli, 1882	1994	1988							van Aartsen & Recevik (1998)
<i>Syrnola lendix</i> (A. Adams, 1863)	1968	1992	1985	1994					Öztürk & Can (2006)
* <i>Trochus erithreus</i> Brocchi, 1821	1980	1988	1996						Galil (2009)
<i>Turbonilla edgari</i> (Melvill, 1896)	1964								Tzomos (2007)
<i>Vexillum depexum</i> (Deshayes in Laborde, 1834)	1997								Zenetos et al. (2003)
<i>Voorwindia tiberiana</i> (Issel, 1869)	1954	1986	1995						Mienis (2004c)
<i>Zafra savignyi</i> (Moazzo, 1939)	1980	1993	1995						Giannuzzi-Savelli et al. (1997)
<i>Zafra selasphora</i> (Melvill & Standen, 1901)	1973								Zenetos et al. (2003), Çinar et al. (2011)
BIVALVIA									
<i>Afrodium richardi</i> (Audouin, 1826)	1997	2000							Zenetos et al. (2003)
<i>Alectryonella crenulifera</i> (Sowerby G.B. II, 1871)	2005								Sharon et al. (2005)
<i>Anadara natalensis</i> (Krauss, 1848)	1935	1985							Zenetos et al. (2003)
<i>Angulus flacca</i> (Roemer, 1871)	1997								Mienis (2004a)
<i>Antigona lamellaris</i> Schumacher, 1817		1988							Engl & Çeviker (1999)
<i>Atactodea glabrata</i> (Gmelin, 1791)	1973					1977			Barash & Danin (1977), Cachia et al. (2004)

TABLE 1. continued

	PS	ST	CY	AS	NA	AD	CM	WM	References
<i>*Barbatia plicata</i> (Dillwyn, 1817)	1978	2004							Tzomos et al. (2010)
<i>*Brachidontes pharaonis</i> (P. Fischer, 1870)	1876	1978	1960	1975		2005	1969	<1971	Zenetos et al. (2003, 2009c) Galil (2009)
<i>Callista florida</i> (Lamarck, 1818)	1932								Ovalis & Zenetos (2007), Manousis et al. (2010)
<i>Chama aspersa</i> Reeve, 1846	2002	1993	2007	2006					Zenetos et al. (2003), Manousis et al. (2010)
<i>Chama pacifica</i> Broderip, 1834	<1905	2000	1998	2005					Manousis et al. (2010) Zenetos et al. (2003), Manousis et al. (2010)
<i>Circenita callipyga</i> (von Born, 1778)	1972								Zenetos et al. (2011)
<i>Clenentia papyracea</i> (Gray, 1825)	1937	1985							Zenetos et al. (2003)
<i>Diplodonta bogii</i> van Aartsen, 2004	1982			2008					Zenetos et al. (2003), Manousis et al. (2010)
<i>Divalvinga arabica</i> Dekker & Goud, 1994	1976								Barash & Danin (1986)
<i>Dosinia erythraea</i> Roemer, 1860	<1905			2007					Zenetos et al. (2003), Manousis et al. (2010)
<i>Fulvia australis</i> (Sowerby G.B. II, 1834)	<1948								Haas (1948)
<i>Fulvia fragilis</i> (Forsskål, 1775)	1938	1986	1983	1998	1990		2008	1991	Zenetos et al. (2009a, 2009c)
<i>Gafrarium pectinatum</i> (Linnaeus, 1758)	<1905	1986	2005						Zenetos et al. (2009a)
<i>Gastrochaena cymbium</i> Spengler, 1783	1954	1990		1974					Zenetos et al. (2003), Manousis et al. (2010)
<i>Glycymeris arabica</i> (H. Adams, 1870)	1966								Manousis et al. (2010)
<i>Hiatula ruppelliana</i> (Reeve, 1857)	<1905								Barash & Danin (1977)
<i>Laternula anatina</i> (Linnaeus, 1758)	<1905	1992							Tillier & Bavay (1905)
<i>Limopsis multistriata</i> (Forsskål, 1775)	1965								Zenetos et al. (2003)
<i>Mactra lilacea</i> Lamarck, 1818	1965								Barash & Danin (1977)
<i>Mactra olorina</i> Philippi, 1846	<1889								Mienis (2002)
<i>Mahvifundus regulus</i> (Forsskål, 1775)	<1929	1973	1970	1999	2001				Zenetos et al. (2003)
<i>Modiolus auriculatus</i> (Krauss, 1848)	1935								Galil (2009), Zenetos et al. (2009c)
<i>Musculista perforabilis</i> (Dunker, 1857)	1960								Haas (1937)
<i>Nanostrea exigua</i> Harry, 1985	2004								Barash & Danin (1972)
<i>Paphia textile</i> (Gmelin, 1791)	1939	1985	2004						Barash & Danin (1972)
<i>Petricola hemprichi</i> Issel, 1869	1900	1999							Mienis (2008)
<i>Pinctada radiata</i> (Leach, 1814)	1874	1982	1899	1961	1890	<1996	1915	<1979	Zenetos et al. (2009a)
<i>Psammotreta praeurupta</i> (Salisbury, 1934)	2008	1992	2009						Zenetos et al. (2003) Zenetos et al. (2009a), Mienis (2010)

TABLE 1. continued

	PS	ST	CY	AS	NA	AD	CM	WM	References
<i>Pseudochama corbieri</i> (Jonas, 1846)	1963			1939					Zenetos et al. (2003), Manousis et al. (2010)
<i>Septifer forskali</i> Dunker, 1855		2001	2005	2010					Zenetos et al. (2009a, 2011)
<i>Sphenia rueppellii</i> A. Adams, 1850	1978	1998							Barash & Danin (1986), Zenetos et al. (2010)
<i>Spondylus spinosus</i> Schreiber, 1793	1988	1991	2001						Zenetos et al. (2009a)
<i>Tellina valtonis</i> Hanley, 1844	1970	1995							Zenetos et al. (2003)
<i>Timoclea marica</i> (Linnaeus, 1758)	1997								Bogi & Gail (1999)
<i>Trapezium oblongum</i> (Linnaeus, 1758)	1980								Mienis (1980b)
CEPHALOPODA									
<i>Octopus aegina</i> Gray, 1849	1934	1992							Salman et al. (1999)
<i>Octopus cyanea</i> Gray, 1849	1997								Mienis (2003b)
<i>Sepia pharaonis</i> Ehrenberg, 1831	2003								Mienis (2003c)
* <i>Septoteuthis lessoniana</i> Férussac, 1831 in Lesson, 1830-1831	2004	2002	2009	2009					Tzomos et al. (2010)

area PS (114) towards area ST (77) and CY (41 species) and then, towards AS (29) while the number of species recorded before 1990 (dark part of the column) is also decreasing in the same direction (PS, 89 species; ST, 36 species; CY, 12 species and, AS, 8 species). On the contrary, the number of species recorded from 1990 onwards is increasing from area PS (25 species) to areas, ST (41 species) and CY (29 species) while it shows a decrease towards area AS (21 species). Furthermore, most of the Lessepsian mollusc species recorded in areas, ST and CY after 1990 have been collected in area PS before 1990, whilst species reported in area AS after 1990 have been reported in area ST either before 1990 or some years before their collection in the Aegean Sea (Table 1).

In respect to area NA, thirteen species of Lessepsian Mollusca have been reported so far. Four of these species have been collected before 1990, while nine of them after 1990. In respect to the latter, they have been recorded from area PS before 1990.

DISCUSSION

A review of the relevant literature shows that the entrance rate of Lessepsian species in the Mediterranean has not been studied in detail. Por (1978) noted that there is no indication that the Lessepsian migration is speeding up while later, Por & Dimentman (2006) argued that there is no evidence that the migratory process is nearing a plateau without however, providing any other information. Madl (1999), considering all Lessepsian groups combined to a heterogeneous unit noted that the process of Lessepsian immigration will eventually reach a plateau but, according to the same author, there were no such indication at that time. He also estimated that the immigration continues at a rate of 5 to 10 species per year.

In respect to specific Lessepsian groups, Koukouras *et al.* (2010) showed that during the period 1869 to 2003, the entrance rate of Lessepsian decapods has been accelerating. Moreover, these authors estimated that during the period 1924 to 2007 the cumulative species number of Lessepsian decapods has been increasing on average by 0.39 species per year. Similarly, Ben Rais Lasram & Mouillot (2009) demonstrated that during the period 1910 to 2006 the entrance rate of Lessepsian fish has been increasing. Based on the results of these authors, during the 1990s, the average number of new Lessepsian fish entering the Mediterranean per annum was 0.7 species, while from 2000 onwards this number has increased to two spe-

cies per annum.

Based on our results, the entrance rate of Lessepsian Mollusca in the Mediterranean is also accelerating. As it has been demonstrated for the period 1869 to 2003, the number of new Lessepsian mollusc species entering the Mediterranean per 15 years is on average increasing. Moreover, during the period 1954 to 2009, the cumulative number of Lessepsian Mollusca has been increasing, by 2 species per year on average. The apparent differences in the entrance rates among the Lessepsian Mollusca and the two other taxonomic groups studied (Ben Rais Lasram & Mouillot, 2009; Koukouras *et al.*, 2010) should probably be attributed to the differences in the mode of life of these taxonomic groups which clearly affect their dispersal capabilities (Por, 1978). Furthermore, these Lessepsian groups have not equally attracted the attention of scientists with the relevant research being more focused towards fish (Azzurro, 2008; Galil, 2009).

Although there are numerous published records on the presence of Lessepsian Mollusca in different areas of the eastern Mediterranean, this information has not been adequately analysed in order to acquire a detailed view on the current geographical distribution of these species and their spatio-temporal dispersal. Based on our results, there is a progressive expansion of the geographical distribution of Lessepsian Mollusca in the Mediterranean towards higher geographical latitudes. For example, 20 out of 21 mollusc species recorded in the Aegean Sea (area AS; Fig. 1) after 1990 have been previously recorded in areas ST and PS before 1990. Thus, these species have reached the Aegean Sea by expanding their geographical distribution towards the north. The increasing trend in the number of species recorded after 1990, along the Lessepsian route should mainly be attributed to the progressive dispersal of the species recorded before 1990. On the other hand, the decrease in the number of species in AS indicates that certain Lessepsian Mollusca have not yet reached the Aegean Sea. In general, the Lessepsian molluscs seem to be gradually expanding their distribution from Port Said both towards the west along the African coast, and towards the east along the coasts of Israel, Lebanon and Syria; from there, towards the southern Turkish coast and the coasts of Cyprus, and finally towards the Aegean Sea. Furthermore, four species have already reached the Adriatic Sea, nine have been collected from the Central Mediterranean (excluding the northern African coast), while six Lessepsian mol-

lusc species have already reached the western part of the Mediterranean (Table 1). Most of the Lessepsian Mollusca are coastal species (Por, 1978; Zenetos *et al.*, 2003) and they expand their distribution moving in shallow waters along coastal areas. A similar pattern of dispersal has been also reported for other Lessepsian groups, such as fish (Tzomos *et al.*, 2007; Ben Rais Lasram & Mouillot, 2009) and decapods (Koukouras *et al.*, 2010).

In respect to the current geographical distribution of Lessepsian Mollusca in the Mediterranean and their spatio-temporal dispersal in the areas of the eastern Mediterranean we can note the following:

Area PS, the most proximate area to Port Said, hosts the highest number of Lessepsian molluscs (114 species) compared to any other of the areas studied. However, sixteen species of Lessepsian molluscs have not yet been reported from this area (Table 1). Two of these species have been reported from the North African coast (area NA), but close to Port Said. Moreover, fifteen of these species have been collected from the southern Turkish coast (area ST), two species were collected at Cyprus and 6 species at Aegean Sea. Thus, the lack of records of these sixteen species from area PS should probably be attributed to the lack of intensive sampling efforts in the Levantine coast (the Sinai Peninsula, Israeli and Lebanese coasts) as well as to the rarity of certain of these species.

The limited number of Lessepsian mollusc species (13) reported from area NA, should probably be attributed to adverse conditions prevailing in the area which interfere with the westward migration of Lessepsian species. Por (1978) argued that migration along the African coast has probably been delayed by the opposing currents, the structure of the outlet at Port Said and perhaps by the Nile water influx. Furthermore, the continuous, high intensity of hydrodynamism due to the long fetch of the North African coast to the prevailing NW winds (Nafaa *et al.*, 1991; Orme, 2005) should be considered another important, adverse factor. Moreover, the area west of Port Said is characterised by large areas of shallow soft substrata, composed of fine sediments originating from older sediment depositions from the Nile and recent subsidence of the delta coast (Orme, 2005). These fine sediments, combined with the high wave action, lead to the creation of large quantities of abioeston in the water column, while the substrate becomes unstable. These factors may also prohibit the westward dispersal of the Lessepsian Mollusca, which

in their majority are benthic inhabitants.

Area ST hosts the highest number of Lessepsian Mollusca after area PS (77 species). It is interesting to note that 49 of these species have reached the southern Turkish coast by expanding their distribution from area PS (Table 1). The number of Lessepsian molluscs known from this area is expected to increase, since more species, already recorded in area PS, will eventually expand their distribution towards the southern Turkish coast, since the latter is a natural continuation of the former. Furthermore, the northward dispersal of the Lessepsian Mollusca along the eastern Levantine coast is probably facilitated by the northward stream that meanders along the coast and generates many eddies having a northward propagation (Alhammoud *et al.*, 2005). These eddies break down at the area of Latakia, east of Cyprus, providing an impulse flux to the Cilician current and to the Asia Minor current, which flow westwards along the southern Turkish coasts (Alhammoud *et al.*, 2005). These two currents seem to play an important role in the westward expansion of the Lessepsian Mollusca along the Anatolian coast.

Cyprus hosts a lower number of Lessepsian Mollusca (41 species) in relation to areas PS and ST. This should be mainly attributed to the isolation of the island from the neighbouring mainland by water masses of great depth which seems to be prohibitive for the arrival of Lessepsian molluscs; in their majority they are shallow-water species. This is also true for other islands in the Eastern Mediterranean such as the island of Crete (Koutsoubas *et al.*, 1992). Furthermore, in the south of Cyprus the temperature of surface waters is rather low as a result of upwelling driven by westerly winds (Alhammoud *et al.*, 2005). These low temperatures might also prevent the arrival of Lessepsian Mollusca, which are thermophilous species. Finally, the rather low number of species reported should also be attributed to the limited sampling effort that has been carried in the area.

The Aegean Sea (area AS) hosts 29 species of Lessepsian molluscs. This, rather low, number should be mainly attributed to the long distance of the Aegean Sea from Port Said, which results in a delayed arrival of Lessepsian species. The first Lessepsian mollusc species [*Pseudochama corbieri* (Jonas, 1846)] was collected at Saronikos Gulf in 1939 (Ralli-Tzelepi, 1946). Up to 1990, only eight Lessepsian molluscs (Table 1) have been reported from the area AS and most of these species were initially collected from the area of Rhodos Island (Barash & Danin, 1989; Zene-

tos et al., 2003). However, during the last ten years certain species have significantly expanded their distribution northwards. In particular, two species of Lessepsian molluscs (*Finella pupoides* A. Adams, 1860 and *Syrnola fasciata* Jickeli, 1882) have expanded their distribution as northerly as Bodrum, at the Aegean coast of Turkey (Öztürk & Can, 2006). Moreover, the bivalve, *Fulvia fragilis* (Forsskål, 1775) has expanded its distribution further north since it has been reported from the Gulf of Izmir (Öztürk & Poutiers, 2005). Recently, Manousis et al. (2010) collected three species of Lessepsian bivalves (*Chama pacifica* Broderip, 1834; *Diplodonta bogi* van Aartsen, 2004 and, *Dosinia erythraea* Roemer, 1860) from Thermaikos Gulf (N. Aegean Sea) which are also new records for the Aegean Sea. Furthermore, they collected a single specimen of the bivalve *Diplodonta globosa* (Forsskål, 1775) which they characterize as a Lessepsian migrant. However, this species should be considered, at least for the time being, as a doubtful Lessepsian migrant, since it has not been previously recorded in the Mediterranean Sea. Furthermore, Manousis et al. (2010) reported two more species of Indo-Pacific origin from Thermaikos Gulf, *Cardites akabana* (Sturani, 1899) and *Chama asperella* Lamareck, 1819. *Cardites akabana* has been previously collected only from Iskederun Bay (southern coast of Turkey) by Çeviker & Albayrak (2006). These authors noted that this species has probably entered the Mediterranean by maritime transport. The bivalve *Chama asperella* has been previously reported from Ashqelon (coast of Israel) and from Saronikos Gulf (Aegean Sea, Greece) (Mienis, 2004a; Ovalis & Zenetos, 2007). However ship fouling is assumed as the most probable mode of introduction in the Mediterranean Sea (Ovalis & Zenetos, 2007). Based on the above data, these two species should also be considered as doubtful Lessepsian migrants and along with *Diplodonta globosa* were not included in Table 1 and our estimates.

According to Por (1978), during the present human-scale historical period the Lessepsian influence could be geographically confined only in the easternmost Mediterranean if drastic climatic changes were not bound to occur. It is now evident that the Mediterranean is becoming warmer as a reflection of the ongoing climate change. For the last decades, the temperature of the western Mediterranean has been rising in deep (Béthoux et al., 1990) and surface waters (Diaz Almela et al., 2007). A similar increase in the mean temperature of the waters of the eastern Mediterranean has also been documented (Raitsos et al., 2010).

The observed increase in the mean temperature of the Mediterranean waters could be considered, at least for the time being, the major factor causing the estimated acceleration of the entrance rate of the Lessepsian Mollusca in the Mediterranean as well as their progressive dispersal towards higher geographical latitudes. Ben Rais Lasram & Mouillot (2009) have also demonstrated that for the period 1910 to 2006, there is a significant positive correlation between the number of newly reported Lessepsian fish per decade and the increasing mean decadal temperature of the Mediterranean waters. Furthermore, a significant amount of evidence has now been accumulated towards an ecological impact of the climate warming on the Mediterranean marine biota (Boero et al., 2008). This evidence include the northward extension and enhancement of native thermophilic species (Francour et al., 1994), the northward dispersal of Lessepsian and other non-indigenous species (Ben Rais Lasram & Mouillot, 2009; Koutsoubas et al., 2009; Raitsos et al., 2010) as well as mass mortality events (Bianchi & Morri, 2000; Cerrano et al., 2000; Bianchi, 2007; Boero et al., 2008).

Based on the existing data, predictions for the future development of the entrance rate of Lessepsian species do not seem to be feasible. This is mainly due to the lack of information on the exact mechanisms that drive this phenomenon. Lessepsian migration is a multifactorial and dynamic process in both space and time.

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